FACTORS AFFECTING THE PHOTOGRAPHIC DETECTION RATE OF GRIZZLY BEARS IN THE SWAN MOUNTAINS, MONTANA

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Abstract: Seven seasonal population estimates were derived from 1989 to 1991 for grizzly bears (*Ursus arctos*) in the Swan Mountains of western Montana using a capture-recapture model for closed populations. Mace et al. (1994) discussed in detail the study design and population modeling procedures which used systematic snaring for initial capture and self-activating cameras for recapture. Twenty-one marked grizzly bears within the camera grids formed the foundation for recapture analysis. We generated 27 photographic records of detections and 71 nondetections in 7 photo sessions. On average, the marked population we sampled was dominated by adult female (29.5%) and adult male (22.6%) grizzly bears. Nearly an equal number of male and female bears were detected on film, but the nondetection sample was skewed towards females (73.3%). Adult males were more frequently detected than adult females or females with young. Most detections (66.6%) were of bears with a prior history of detection. Adult males moved greater distances and consequently encountered more camera stations than other age-gender classes. Generally, movements for all age-gender classes were greatest during the spring and decreased thereafter. When the 7 photo sessions were pooled, it was shown that grizzly bears were not exposed to many camera stations ($\bar{x}$ = 1.6, SD = 1.8) and bears we successfully detected were confronted with significantly more stations ($\bar{x}$ = 2.30, SD = 2.3) than those we failed to detect ($\bar{x}$ = 1.30, SD = 1.44). Logistic regression showed that detections decreased over time. We concluded that differential movement patterns among age-gender classes played an exceedingly important role in photographic detection. The precision of population estimates could be improved by grid densities >5-8 camera station/100 km^2 for grizzly bear populations with similar age-gender structure. Recommendations to increase and sustain precision of population estimates using cameras are provided.

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Grizzly bear population size is notoriously difficult to enumerate for biological and logistical reasons (Harris 1986). However, recent advances using portable, self-activating cameras (Mace et al. 1994) to resight (recapture) grizzly bears demonstrated that meaningful population estimates can be derived in mountainous habitats. Systematic grid snaring was used for initial capture and systematically deployed cameras were used for resightings. Mace et al. (1994) evaluated accuracy and bias of several closed population models using resighting data from 6 camera sessions and concluded that Monte Carlo procedures (Minta and Mangel 1989) provided an accurate measure of population size.

In this paper, we evaluate the effects of several biological factors on photographic detection. Specifically, we evaluate detection in terms of each bears' gender, age-class, reproductive status, history of photographic resighting, average distance moved during photo sessions, and the number of cameras available per individual.

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STUDY AREA

The 516 km^2 core study area, where photographic detection was evaluated, was located in the Swan Mountains (South Fork of the Flathead River drainage) in western Montana and extended from Pioneer Ridge on the north to the Bob Marshall Wilderness boundary on the south (Fig. 1). The western boundary of the core area was bounded by the Swan Mountain Divide, and the eastern edge was Hungry Horse Reservoir.

The study area was located within the Rocky Mountain Cordillera and elevations varied from 914 to 2,736 m. Closed conifer habitat dominated >50% of the area with the remaining habitats classified as rock land, avalanche chute, shrub land, riparian zone, and cutting unit (Mace et al. 1994).

METHODS

Capture, Recapture, and Telemetry Procedures

Grizzly bears were initially captured during the

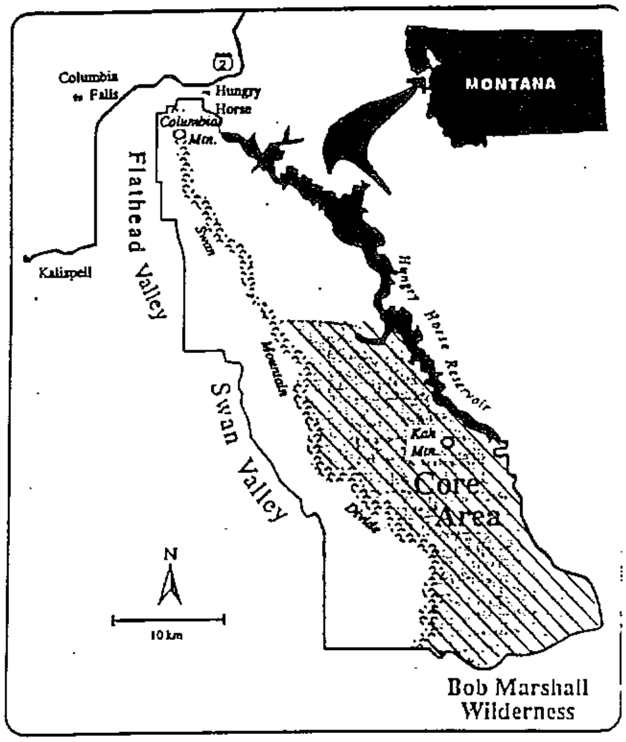

Fig. 1. Map of the study area in the Swan Mountains of western Montana.

spring of 1988-91 using leg-hold snares placed in a systematic grid (Mace at al. 1994). Captured bears were immobilized with either titelamine with zolazepam or ketamine with xylazine. Each bear was fitted with ear tags and 2 unique 16.5 cm by 5 cm Armortite ear streamers for recognition in photographs. Ages were determined by cementum analysis (Stoneberg and Jonkel 1966). Individual grizzly bears >1 year old were fitted with temporary radio collars (Telonics, Inc. Mesa Ariz.) utilizing a cotton spacer for long-term bear safety (Hellgren et al. 1988). One independent yearling was instrumented as well.

Grizzly bears were photographically detected using self-activating camera units (Mace et al. 1994). Each unit consisted of a 35 mm camera with flash, a passive infrared sensor, and a 12-volt battery. Thirty-six exposure print film was used.

We conducted 7 sampling periods between 1989 and 1991 using a systematic design at grid densities of between 5 and 8 cameras/100 km^2. Three photo sessions per year were conducted in 1989 and 1990, and one spring session was conducted in 1991. The spring session each year occurred when grizzly bears were generally consuming herbaceous vegetation and carrion. We again deployed cameras during the height of the berry season when grizzly bears were foraging on the fruit of globe huckleberry (*Vaccinium globulare*) and serviceberry (*Amelanchier alnifolia*). Cameras were again deployed in the autumn after most berry foraging had ceased and bears were again consuming vegetation and some large mammals. Naive population density estimates for marked bears varied between 2.3-3.29 independent grizzly bears/100 km^2 during each sampling period.

The grizzly bear population was photographically sampled at similar times each year (Table 1). Attractant baits were weighed to ensure consistency among photo stations. Additional lures were used at each photo station and varied among sessions and years (Table 1). Sampling effort per photo station, termed "station grid-nights" was defined as the sum of all portions of a 24-hour day that a photo station was functional during the period when all other stations were deployed. Station grid-nights were then summed to give a total for the entire photo session.

Each photo station was composed of 3 trees forming a triangular pattern. The attractant bait was hung between 2 trees and the camera unit was secured approximately 3.5 m up the third tree and aimed at the ground below the bait. Cameras were deployed and monitored by foot, all-terrain vehicle, truck, and a Hughs 500 helicopter; visits to stations were minimized.

As weather permitted, we obtained a minimum of 3 aerial telemetry locations on each bear during each session using a Cessna 180 or 182. Bear location and

Table 1. Camera deployment dates and lures used to detect grizzly bears in the Swan Mountains, Montana, 1989-91.

Session number	Session dates	Number cameras	Grid nights	Weight of bait kg[a]	Lure[b]
1	9 Jul-17 Jul 1989	27	201	43	1
2	22 Aug-4 Sep 1989	28	347	41	1
3	6 Oct-17 Oct 1989	40	465	15	2
4	11 Jul-22 Jul 1990	27	397	15	3
5	17 Aug-30 Aug 1990	28	356	15	4
6	27 Sep-14 Oct 1990	27	468	15	5
7	19 Jun-21 Jul 1991	29	725	15	2

[a] domestic or wild ungulate meat
[b] 1: blueberries and 3.7 liters of livestock blood
2: blood only
3: blood and anise extract
4: blood and vanilla extract
5: blood and "Canine Call" (commercial skunk scent)

photo station UTM coordinates were entered into the computer-aided graphics program SURFER (Golden Software Inc.) for spacial analyses.

Analysis Procedures

Twenty-one marked grizzly bears provided photographic information for all or a portion of 7 photo sessions. Each individual was classified as either being photographically detected or not during each session. An individual was termed "detected" if it was photographed at least once during a photo session. Grizzly bears were considered to be within a grid and available for detection if >50% of each bears' locations during a photo session was within the boundary of the grid area.

Photographic detections were evaluated for each bear and session. Bears were classified by gender and age-class. Adults were those reproductively mature animals ≥5 years old with the exception of one 3-year-old female. Subadults were independent animals 2-4 years old but included one weaned yearling. Bears were classified as moving through the environment either alone or as a family group. Family groups were classified as a single unit in terms of photo detection as offspring did not move independently of their mother.

Prior history of photographic resighting was used to separate those individuals who had been detected during previous sessions from those who had not. This variable was not applied to multiple resightings within a photo session. The first photo session (1-1989, Table 1) was deleted from this analysis as there were no prior sessions.

Some grizzly bears learned to chew the rope suspending the attractant bait and were consequently rewarded. For each photo session we classified each bear as having been rewarded during previous sessions or not.

The number of photo stations potentially available to each grizzly bear during a session was estimated. Convex polygons were constructed from aerial telemetry locations and from photo station coordinates where bears were successfully photographed. To increase the number of location points per bear, and to more accurately evaluate the spacial relationship between bear and photo grid, we included telemetry locations ±10 days from the inclusive grid dates. When possible, we developed convex polygons for marked grizzly bears not wearing functional radio transmitters if they visited at least 3 photo stations. For those nonradioed bears photographed at <3 stations, we used the number of stations where they were detected.

The number of cameras available to each bear also depended on the performance of cameras. Performance problems occurred because of mechanical failure, harsh site conditions, inclimate weather, and interference by other species of wildlife. Therefore it was possible that grizzly bears visited some baited stations when cameras were not functioning or all frames were exposed from other causes. As a correction factor, we eliminated 12 of 207 (5.7%) photo stations that functioned <50% of the time.

Average daily movements (ADM) in meters were generated for each bear and session using distance measurements derived from consecutive aerial telemetry data. Average ADM's were then derived for each age-gender class for each photo session.

Contingency data were evaluated using Pearson's χ^2 with the Yate's correction for small samples (Sokal and Rohlf 1969). The variables ADM and number of cameras available were compared among 5 age-gender classes using Mann-Whitney (MW), Kruskal-Wallis (KW), and KW one-way analysis of variance procedures. Nonlinear logistic regression was used to evaluate the frequency of detection through time. We selected a maximum likelihood probit estimation (MLE) procedure (Agresti 1990) using the software package SYSTAT (Systat Inc. 1988).

RESULTS

The grizzly bear population we sampled 7 times with cameras was dominated by adults ($\bar{x}$ = 71.4%) (Table 2). Adult females ($\bar{x}$ = 29.5%) and adult males ($\bar{x}$ = 22.6%) were the most prevalent age-gender classes. Relatively few subadult males were present in the population and an average of 19.4% of the population was family groups.

The 21 individual grizzly bears generated 27 (27.5%) records of photographic detection and 71 (72.5%) records of nondetection from the 7 photo sessions. Fifty-seven percent of the original marked population (from session 1) was still alive or within the core study area by Session 7.

Seventy percent and 72% of the detections and nondetections, respectively, were of adult animals (Table 3). Therefore, we rejected the null hypothesis that photographic detection was independent of the frequency of adult and subadults in the population (χ^2 = 0.00, df = 1, P = 1.0). Male and female grizzly bears were almost equally represented in the sample of photographic detections (Table 3), although most (73.2%) of the nondetections were female bears. The null hypothesis that frequency of detection was

Table 2. Summary of population characteristics for marked grizzly bears sampled through photography, Swan Mountains, Montana.

	Number of marked grizzly bears in photo grid during each of 7 photo sessions								
Age-gender class	1	2	3	4	5	6	7	$\bar{x}$	$\bar{x}$%
Adult	9	10	8	11	11	11	10	10.0	74.1
Subadult	5	2	2	5	6	6	2	4.0	28.6
Male	4	4	3	5	6	6	4	4.6	33.0
Female	10	8	7	11	11	11	8	9.4	67.0
Adult male	3	4	3	3	3	3	3	3.1	22.6
Adult female	3	4	3	6	6	6	1	4.1	29.5
Family group	3	2	2	2	2	2	6	2.7	19.4
Subadult male	1	0	0	2	3	3	1	1.4	10.1
Subadult female	4	2	2	3	3	3	1	2.6	18.7

Table 3. Summary of contingency data regarding the age and gender of marked grizzly bears and frequency of photographic detection (n = 27 detectimns and n = 71 nondetections). Swan Mountains, Montana.

	Number of cases			
Age-gender class	Detected	Not detected	% detected	Significant χ^2 test[a]
Adult	19	51	27.1	
Subadult	8	20	28.6	
Male	13	19	40.6	
Female	14	52	21.2	
Adult male	11	11	50.0	A B
Adult female	6	23	20.7	A
Family group	2	17	10.5	A B
Subadult male	2	8	20.0	A
Subadult female	6	12	33.3	A

[a] Those age-gender classes with the same letter were significantly different in frequency of detection and nondetection using the χ^2 test with $P < 0.05$.

independent of gender was not significant ($\chi^2 = 3.15$, df = 1, $P = 0.076$).

We rejected the null hypothesis that frequency of detection was independent of the 5 age-gender classes ($\chi^2 = 9.601$, df = 4, $P = 0.048$). However, only 1 of 10 age-gender subsets was significantly different (Table 3). The frequencies of detection between adult males and adult females were significant ($\chi^2 = 3.607$, df = 1, $P = 0.058$) and frequency differences between adult males and family groups were significant ($\chi^2 = 5.627$, df = 1, $P = 0.002$).

Eighty-one percent of the 98 photographs were of solitary animals, and these independent individuals comprised the majority (92.6%) of the detection sample. In only 2 of 19 (10.5%) cases were family groups detected. The hypothesis that frequency of resighting was independent of unit status was not rejected ($\chi^2 = 2.446$, df = 1, $P = 0.118$).

We assessed the relationship between prior history of detection and its effect on detection during later sessions (omitting session 1-1989). Most of the 21 detections (66.6%) were of bears who had been photographed before. However, previous detection did not ensure that grizzly bears would continue to be detected, as 47.6% of the records showed that bears with prior detections were not photographed ($\chi^2 = 1.591$, df = 1, $P = 0.207$). In most instances, grizzly bears were unsuccessful in actually obtaining the hanging bait (85 of 98 cases, 86.7%). However, those bears with a history of reward were more likely to be detected during a later session than not (69.2%).

Adult males moved greater distances (n = 17, $\bar{x}$ = 2,092 m, SD = 1,347 m) during the photo sessions than other age-gender classes (Table 4). Family groups moved the least (n = 18, $\bar{x}$ = 942 m, SD = 346 m). The KW-ANOVA suggested that variation in the distance moved varied among the 5 age-gender classes (F-ratio = 5.941, df = 4, $P = 0.000$). Adult males moved farther than solitary adult females (MW-U = 376.0, df = 1, $P = 0.001$), subadult females (MW-U = 236.0, df = 1, $P = 0.006$), and family groups (MW-U = 272.0, df = 1, $P = 0.001$). With the exception of subadult males which showed a slight increase in ADM between spring and summer, other age-gender class decreased their movements as the active season progressed. Average daily movement's for spring, summer, and autumn using all bears were 1,537 m (SD = 1,020 m), 1,228 m (SD = 775 m), and 894 m (SD = 615 m) respectively. When age-gender classes were pooled for each season, seasonal movements were significantly different (KW = 9.153, df = 2, $P = 0.01$).

The 5 age-gender classes were exposed to variable number of photo stations (Table 5) and the null hypothesis that numbers of cameras available to each class were equal was rejected (KW = 11.55, df = 4, $P = 0.021$). Adult males were exposed to more

Table 4. Seasonal average daily movements (m) of marked grizzly bear during photo sessions (n, $\bar{x}$, SD) in the Swan Mountains, Montana.

Season	Average daily movement by age-gender class				
	Adult male	Adult female	Subadult male	Subadult female	Family group
Spring	8	10	4	8	10
	2,352	1,157	1,188	1,354	1,003
	1,960	334	613	475	283
Summer	5	10	3	5	4
	1,920	741	1,840	1,352	964
	294	548	1,335	670	560
Autumn	4	8	3	5	4
	1,786	736	1,007	653	769
	502.	717	385	308	269
Total	17	28	10	18	18
	2,092	1,042	1,329	1,159	942
	1,347	665	827	570	346

cameras than adult females (MW-U = 358.0, df = 1, P = 0.029), than family groups (MW-U = 342.0, df = 1, P = 0.000), and subadult females (MW-U = 317.0, df = 1, P = 0.001).

Male grizzly bears were exposed to more (n = 28, $\bar{x}$ = 2.4, SD = 2.3) camera stations than females (n = 66, $\bar{x}$ = 1.2, SD = 1.40) and differences were significant (MW-U = 560.0, df = 1, P = 0.002). Adults were exposed to more stations (n = 65, $\bar{x}$ = 1.6, SD = 1.9) than subadults (n = 29, $\bar{x}$ = 1.4, SD = 1.28) but differences were insignificant (MW-U = 877.0, df = 1, P = 0.767). Solitary bears also were exposed to more stations (n = 75, $\bar{x}$ = 1.6, SD = 1.7) than family groups (n = 19, $\bar{x}$ = 1.3, SD = 1.9) but differences were not significant (MW-U = 540.0, df = 1, P = 0.10). Overall, grizzly bears in our study were not exposed to many camera stations (n = 93, $\bar{x}$ = 1.60, SD = 1.80) and in 21.5% of the cases had no cameras within their polygons. In 94% of the cases, bears had <4 cameras within their polygon.

Grizzly bears detected by camera were confronted with more camera stations (n = 27, $\bar{x}$ = 2.30, SD = 2.3) than bears we failed to detect (n = 71, $\bar{x}$ = 1.27, SD = 1.44) and these differences were significant (MW-U = 588.0, df = 1, P = 0.007).

The proportion of the marked grizzly bear population successfully detected decreased over time (photo sessions) even though new bears were added to the marked sample each year. Although there were some changes in the demographics of the focal population, bears were exposed to similar number of cameras each session (KW = 4.389, df = 6, P = 0.624). The MLE logistic regression showed a loss function of -0.250 for detections of marked grizzly bears. The estimated proportion of marked bears detected per session decreased from approximately 54% during photo session 1, to 8% during session 7 (Fig. 2).

Table 5. The number of camera stations within grizzly bear convex polygons in the Swan Mountains, Montana.

Number cameras per polygon	Age-gender class				
	Adult male	Adult female	Subadult male	Subadult female	Family group
n	18	28	10	19	19
minimum	0	0	0	0	0
maximum	9	10	6	2	3
mean	2.7	1.4	1.9	1.0	0.9
SD	2.4	2.0	1.9	0.7	0.8
Significant[a]	A	A	A	A	A
	B	B			
	C			C	
	D				D

[a] Those age-gender classes with the same letter were significantly different using the MW-U test with P < 0.05.

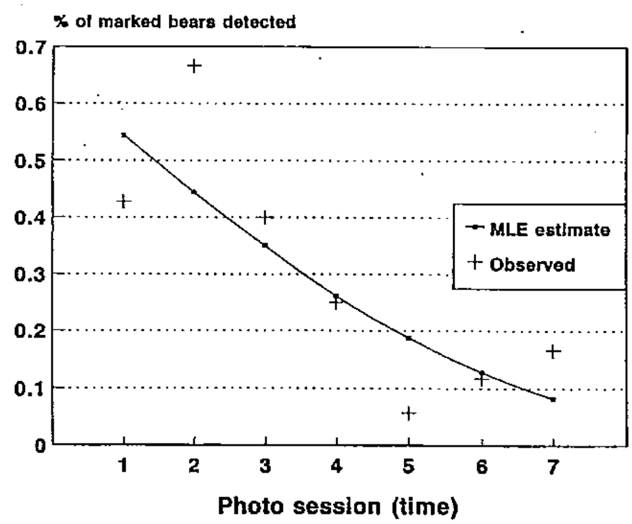

Fig. 2. Results of logistic regression showing decline in frequency of photographic detection of grizzly bears over 7 photo sessions, Swan Mountains, Montana.

DISCUSSION

Several, often compounding sources of bias are common to all capture-recapture experiments with wildlife. These include behavioral responses, heterogeneity in the response of individuals to capture-recapture methods, and the effect of time (White et al. 1982). These biases are especially acute and difficult to measure for grizzly bears because of inherently low capture and recapture sample sizes. Coupled with the difficult terrain this species inhabits, it is no surprise that population estimates and measures of bias for grizzly bear populations are rarely obtained. We attempted to learn, as quickly as possible, the effectiveness of self-activating cameras for recapturing grizzly bears and sampled the same population 7 times in 3 years.

Using cameras to recapture grizzly bears had several advantages over other recapture techniques such as snares (Mace et al. 1994). First, the assumptions of closed population modeling can be more easily met by maximizing coverage of an area with cameras over a short period when population demographics are stable (e.g., no death, immigration). The shorter duration a sampling session is conducted, the more likely critical assumptions will be met. Second, bias due to catchability can be reduced through the use of an alternative recapture technique (Seber 1982), in this case cameras. Third, bias due to human odor and presence is minimized. Fourth, no physical restraint of bears is necessary, eliminating possible injury or death to bears from handling.

It was our intent to isolate those factors affecting photographic detection. Perhaps the greatest surprise to us was the low number ($\bar{x}$ = 1.60) of cameras available to individual grizzly bears given an ADM of over 1,000 m for all age-gender classes. In 21.5% of the cases grizzly bears moved within either the synusia or along the periphery of photo grids and were unavailable for detection. These estimates of camera numbers within polygons were optimistic because we included locations $\pm$10 days surrounding the grid-deployment dates. Our use of camera grid densities of between 5 and 8 cameras/100 km^2 obviously did not maximize the opportunity for grizzly bears to locate the baited photo stations. We believe that much of the variation in photographic detection among age-gender classes was explained by relationships between ADM and camera grid densities. Increasing the density of cameras within the sampling area would probably increase detection rates.

Male and female grizzly bears were nearly equally represented in the photographic detection sample, but far more of the nondetections were of female bears because females on average moved less and consequently encountered fewer photo stations. The frequency of detection varied significantly among age-gender classes. Adult males were resighted more often than adult females and females with young. Subadult females and males appeared to be detected in proportion to their presence in the population. We believe that detection frequencies would differ among populations with different demographics, densities, and movement patterns.

Mace et al. (1994) discussed several other factors which appear to influence photographic detection. During the summer, better detection of grizzly bears occurred when the globe huckleberry crop was poor and bear movements increased. The authors also cautioned that late autumn sampling was negatively influenced by snow, freezing temperatures, or prehibernation lethargy (Nelson et al. 1983).

We believe that both marked and unmarked grizzly bears were confronted with a novel technique during the early photo sessions and that interest in the baited sites decreased as more sessions were conducted. To date, we relied on olfactory cues to attract bears to the photo stations. However, there are other alternatives such as auditory stimuli (e.g., predator or fawn calls) that may prove equally effective. We believe that a long-term program to estimate population size would benefit by presenting bears with a variety of attractants. If the chosen capture-recapture model allows for unequal recapture probabilities, rewarding bears with some bait may help retain adequate photo detection rates over time. Furthermore, we believe that population monitoring programs would benefit by deploying cameras less frequently than described here (e.g., once per year).

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